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NOMENCLATURAL NOTES ON THE LAND SNAIL GENUS BOTHRIEMBR YON PILSBRY, 1894 (PULMONATA: BULIMULIDAE), WITH REDESCRIPTIONS OF THE TYPE AND TWO OTHER SPECIES

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ABSTRACT

Corrected names and revised synonymies are presented for 3 species of *Bothriembryon*, including the type species *B. melo* (Quoy and Gaimard, 1832). Type specimens are designated, and diagnoses of the species and genus presented.

INTRODUCTION

Bothriembryon is a genus of Australian bulimulid land snails comprising not less than 30 living species, most of which are polymorphic and geographically variable. The type species, Helix melo Quoy and Gaimard, 1832, is one of the more variable of these and its identity has been a subject of some confusion for many years. Our studies have shown that *B. melo* is restricted to the Albany — Bremer Bay districts of southern Western Australia. Two other species that have been confused directly or indirectly with it inhabit the Shark Bay district on the central western coast, one of them ranging southward to the Lower Murchison district. For the smaller of these two species, we propose to use the name *B. costulatus* (Lamarck, 1822) and for the larger, the name *B. onslowi* (Cox, 1864). Other names that have been previously used in connection with these three species include Helix (Cochlogena) costulata Férussac, 1821, Helix (Cochlogena) melones Férussac, 1821, Bulimus inflatus Lamarck, 1822, Bothriembryon castaneus Pilsbry, 1900 and Bothriembryon minor Pilsbry, 1900.

Except where otherwise stated, all specimens referred to in this paper are in the collection of the Western Australian Museum.

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HISTORICAL SUMMARY

The nomenclatural problems that we seek here to clarify seem to have arisen from the disregard by some early collectors and taxonomists for locality data and from the mixing of specimens from different localities in the early collections. The initial confusion affecting the species costulatus and melo appears to have stemmed from labelling errors and the mixing of samples collected by M.F. Péron and C.A. Lesueur in 1801 while at Shark Bay ('la baie des Chiens-Marins') and in 1803 at King George Sound ('le port du Roi George'). The expedition, commanded by T.N. Baudin, visited the western part of Australia on two occasions, initially on the vessels 'Géographe' and 'Naturaliste' and subsequently on the 'Géographe' and 'Casuarina'. Péron prepared a narrative of the voyage (Péron, 1807) but did not live to finish it and it was left to L.C. de Freycinet, a senior officer of the expedition, to bring the work to completion (Whittell, 1954: 59). The extensive collections of Peron and Lesueur were brought to Paris and deposited in the Museum National d'Histoire Naturelle, where they were later studied by Férussac, Lamarck and others. However, Lamarck acquired some of the shells of Péron and Lesueur for his personal collection. These, which include the type material of Bulimus costulatus Lamarck, are now in the Muséum d'Histoire Naturelle, Geneva.

In 1818, de Freycinet returned to Australia in command of the 'Uranie', accompanied by the naturalists J.R.C. Quoy and J.P. Gaimard. Collections were made by them at Shark Bay but these were lost by shipwreck at the Falkland Islands, with the exception, it seems, of a few specimens saved from the wreck by C. Gaudichaud, the ship's apothecary (Iredale, 1939). Gaudichaud's shells, which apparently included specimens of *Bothriembryon*, later passed into the hands of Férussac, but are now believed to be lost.

In 1826, Quoy and Gaimard returned to the western part of Australia, this time to King George Sound, on the 'Astrolabe', commanded by J. Dumont d'Urville. (Their visit preceded by only a few months the establishment of a permanent British settlement at Albany under Major E. Lockyer toward the close of that year.) The type material of *Helix melo* was collected on this occasion and was described, together with the other zoological results of the voyage, by Quoy and Gaimard (1832). Their collection is in the care of the Paris Museum.

The species Bothriembryon onslowi (Cox, 1864) was described from a shell collected on Dirk Hartogs Island by a Captain Onslow of the vessel 'Gazelle' and is now in the Cox Collection at the Australian Museum, Sydney. It enters this study as a result of having been confused with *B. costulatus* (Lamarck) by Iredale (1939).

Summaries of the early voyages mentioned above have been made by Alexander (1916) with regard to general Western Australian zoology and by Iredale (1939) concerning land snails. We propose initially to discuss in turn eight nomina, their types and status and to follow these with consolidated redescriptions of the three biospecies which underly them.

THE NAMES, TYPES AND LOCALITIES

1. Helix (Cochlogena) costulata Férussac, 1821

Tableaux Systèmatiques des animaux mollusques. Limaçons, p. 58, January 1821; p. 54, June 1821. Localities given as: 'La Port du Roi George, dans la Nouvelle-Hollande, PERON; la baie des Chiens-Marins, GAUDICHO'.

As Iredale (1939) has pointed out, the name costulata Férussac is a nomen nudum but, because later workers quoted Férussac's localities, the identity of his specimens is of interest. In June 1965, one of us (B.R.W.) searched without success the collection of the Museum National d'Histoire Naturelle, Paris, for the Shark Bay specimens attributed by Férussac to Gaudichaud and which were saved by him from the 'Uranie' wreck. We presume these specimens to be lost. There is, however, in that collection a sample of 8 shells which according to the label are types of 'Helix costulata Fér'. The label bears the names of Péron and Lesueur as collectors and the locality 'Port du Roi George'. We consider this locality to be erroneous because 7 of the 8 shells belong to the smaller of the two species which occur in the Shark Bay district, i.e. B. costulatus (Lamarck). The largest of these shells is shown in Pl. III, fig. 5a, b. The eighth shell is a viviparid, probably not Australian, which seems to have been included in the sample in error. It is noted that the original Férussac catalogue lists only 7 specimens of 'H. (C.) costulata'.

We are of the opinion that the 7 specimens comprising the type series of H. (C.) costulata Férussac in Paris represent part of the sample collected by Péron and Lesueur, not at King George Sound in 1803 but at Bernier and possibly other islands at Shark Bay in 1801. This conclusion is discussed more fully below.

2. Bulimus inflatus Lamarck, 1822

Histoire naturelle des animaux sans vertèbres 6 (2): 122. Locality given as 'dans la Nouvelle-Hollande'. Figured Delessert, 1841, Recueil de coquilles décrites par Lamarck, pl. 28, fig. 1 a, b.

Lamarck's description of Bulimus inflatus included the words 'Mon cabinet', indicating that there were specimens in his personal collection.

The five shells comprising this lot are now in the Muséum d'Histoire Naturelle at Geneva, the largest of them (26.0 mm in height) being that figured by Delessert and selected as the lectotype by Mermod (1951: 728,

PLATE I

Bothriembryon melo (Quoy and Gaimard)

Figs. 1a, 1b: Lectotype; Bald Head near Albany (morph a) Museum National d'Histoire Naturelle, Paris.

Figs. 2a, 2b: Paralectotype, 'varietas castanea; vitta alba cincta'; Bald Head near Albany (morph e) Museum National d'Histoire Naturelle, Paris.

Figs. 3a, 3b: Lectotype of *Bothriembryon castaneus* Pilsbry; probably from Doubtful Island (morph e) Australian Museum C87458.

Figs. 4-6: All from Limestone Head near Albany.

Figs. 4a, 4b: Numerous intense brown stripes, with an obscure brown peripheral band (morph a) WAM 248-72.

Figs. 5a, 5b: Pallid, with few brown stripes and obscure multi-spiral white bands, probably the result of injury to the mantle edge (morph a) WAM 248-72.

Figs. 6a, 6b: Diffuse yellow-brown with few brown stripes (morph a) WAM 1533-70.

PLATE II

Bothriembryon melo (Qyoy and Gaimard)

Figs. 1-4: All from Frenchman Bay, Albany.

Figs. 1a, 1b: Straw-yellow with chestnut subsutural band and umbilicus (morph b) WAM 1-72.

Figs. 2a, 2b: Brown striped and banded on a yellow-brown ground (morph a) WAM 1-72.

Figs. 3a, 3b: Same as Fig. 2 but with a white peripheral band (morph f) WAM 1-72.

Figs. 4a, 4b: Chestnut with a white peripheral band (morph e) WAM 236-72.

Figs. 5a, 5b. Breaksea Island. Diffuse straw-yellow with pale pink columella (morph d) WAM 246-72.

Figs. 6a, 6b: Waychinicup River Valley. Diffuse dark yellowish-brown (morph C) WAM 249-72.

PLATE III

Bothriembryon melo (Quoy and Gaimard)

Figs. 1a, 1b: Near Hunter River estuary, Bremer Bay. Brown with straw-yellow axial flames and dark brown umbilical patch (morph g) WAM 266-70.

Figs. 2a, 2b: Locality as for Fig. 1. Intense dark brown with thin axial yellow flames and light brown peripheral band (morph h) WAM 266-70.

Figs. 3a, 3b: Bremer Bay. Diffuse medium brown, without flames, with strong white peripheral band (morph e) WAM 238-72.

Bothriembryon costulatus (Lamarck)

Figs. 4a, 4b: Lectotype. Probably from Bernier Island, Shark Bay. Faded off-white with white flames. Museum d'Histoire Naturelle, Geneva 1092/65.

Figs. 5a, 5b: Largest of the type series of *Helix* (Cochlogena) costulata Ferussac. Probably from Bernier Island, Shark Bay. Faded, pale greyish-brown with white flames. Museum National d'Histoire Naturelle, Paris.

Figs. 6a, 6b: Types of *B. minor* Pilsbry. Locality unknown. Academy of Natural Sciences of Philadelphia 78504.

PLATE IV

Bothriembryon costulatus (Lamarck)

Figs. 1-5: Dirk Hartogs Island, Shark Bay. Coll. J.J. Walker, 13.xi.1890 (Smith, 1895: 95). Five faded shells glued to dark paper; apparently one shell missing. British Museum (Natural History) 91.11.21. 144-9.

(Contd. on page 306)













Map 1: Western Australia. Areas studied.



Map 2: Western Australia. Torbay to Pt Charles, showing localities for Bothriembryon melo.



Map 3: Western Australia. Kalbarri to Pt Cloates, showing localities for *Bothriembryon* costulatus.



Map 4: Western Australia, Shark Bay district. Bothriembryon onslowi localities.

(Plate IV Contd.)

Figs. 6a, 6b: False Entrance Well, Carrarang. Light brown with pale flames and white circumbilical band. WAM 1514-70.

Figs. 7a, 7b: Bernier Island, northern end near old hospital site. Light brown with white flames; slightly faded. WAM 342-73.

Figs. 8a, 8b: 13 miles from Carrarang homestead along road to Useless Loop, Shark Bay. Diffuse pale pinkish-brown with few white flames and white circumbilical area. WAM 109-68.

Figs. 9a, 9b: Dorre Island, Shark Bay. Medium brown with white flames and white circumbilical area; slightly faded. WAM 230-73.

Figs. 10a, 10b: Red Bluff, 5 miles south of Kalbarri (near southern end of range). Medium brown with white flames; slightly faded. WAM 475-48.

Figs. 11a, 11b: Bill Bay, 2 miles south of Pt Maud, Cardabia (near northern end of range). Pale waxen pinkish-brown with white flames. WAM 1524-70.

PLATE V

Bothriembryon onslowi (Cox)

Figs. 1a, 1b: Holotype. Dirk Hartogs Island, Shark Bay. Yellowish-brown with diffuse paler flames. Australian Museum C84882.

Figs. 2a, 2b: Dirk Hartogs Island, collected J.J. Walker (Smith, 1895: 95). The larger of two faded shells. British Museum (Natural History) 91.11.21. 202-4.

Figs. 3a, 3b: Monkey Mia, Peron Peninsula. Chestnut-brown with contrasting yellow flames. WAM 229-73.

Figs. 4a, 4b: False Entrance Well, Carrarang. Chestnut-brown with wavy yellow flames. WAM 1513-70.

Figs. 5a, 5b: 7 miles south of Useless Loop. Diffuse brown with obscure whitish flames. WAM 2232-69.

fig. 78). Like the 7 Paris shells in the type series of *costulata* Férussac, all 5 of the Geneva shells represent the smaller of the Shark Bay species of *Bothriembryon* (see Table 1) and in our view could well have originated from the same source. Lamarck did not identify the source of these specimens but it seems a reasonable assumption that this was Péron and Lesueur.

In his journal Péron (1807: 120) recorded that on June 29th, 1801 at Bernier Island, Shark Bay, 'Two species of land shells extremely numerous, but all dead, occupied great stretches of the interior of the island, one was a small species of *Helix*, the other belonged to the genus *Bulimus* of M. de Lamarck' (quoted in translation from Alexander, 1916: 96). Péron and his colleagues also went ashore on Dorre and Dirk Hartogs Islands and noted the general similarity of all three, but his references to modern land snails relate explicitly only to Bernier Island.

As far as we can determine from samples in the collection of the Western Australian Museum, only one species of *Bothriembryon* occurs today on Bernier and Dorre Islands. This is the smaller of the two Shark Bay species and is without doubt the 'Bulimus' referred to by Péron. The small 'Helix' appears to be the camaenid Rhagada torulus (Férussac, 1819), which occurs on Bernier, Dorre and Dirk Hartogs Islands and also on parts of the adjacent mainland.

It seems clear that Péron and Lesueur collected a sample of Bothriembryon shells while on Bernier Island. This sample, which may or may not have been supplemented with similar shells from Dorre and Dirk Hartogs Islands, we suggest was probably divided at some later time between Férussac and Lamarck. If so, the 7 Paris shells, i.e. the types of costulata Férussac, would then represent Férussac's share of this division, while the 5 at Geneva would be those secured by Lamarck, to become the types of inflatus Lamarck.

The view held by some later workers, for example, Hedley (1892, 1916) and Pilsbry (1900) that *inflatus* Lamarck was a species of the Albany district, may have arisen from a misinterpretation of Delessert's illustrations and perhaps also from reliance on the locality data for *costulata* Férussac, which we have shown above to be partly erroneous. However, Cox (1864, 1868) clearly distinguished between *inflatus* Lamarck, *melo* Quoy and Gaimard and his own new species, *onslowi*.

Iredale (1939) pointed out that the name Bulimus inflatus Lamarck, 1822 is a primary homonym of Bulimus inflatus Olivier, 1801.

3. Helix costulata Lamarck, 1822

Histoire naturelle des animaux sans vertébres 6 (2): 122 (in synonymy).

Evidently Lamarck realized that the specimens which he proposed to name *inflatus* were conspecific with those called *costulata* by Férussac (without description) for he cited that name in the synonymy of *inflatus*. Having shown that *inflatus* Lamarck is not an available name, Iredale (1939) employed *costulatus* as a name introduced in synonymy by Lamarck (see Article 11 (d) of the International Code of Zoological Nomenclature). Both names, *inflatus* Lamarck and *costulata* Lamarck, have the same type specimens, that is, the sample of 5 shells at Geneva.

Iredale (1939) deduced correctly that *inflatus* Lamarck and *costulata* Lamarck apply to 'the Shark Bay shell' but he did not take into account that there are two species of *Bothriembryon* living in that district and assigned these names to the wrong one, that is, the larger species, which we consider to be correctly named *onslowi* Cox. In his 1939 review of the genus, Iredale shows evidence of a change of mind on this question, for on p. 16 he cites *onslowi* as the type species of his subgenus *Hartogembryon* and later, on p. 26, lists *onslowi* in the synonymy of *costulatus*. This allocation seems to have been made without reference to both of the types and, like others before, Iredale may have been misled by Delessert's illustrations, which are not good likenesses of the specimen and species. Lamarck's type is an exceptionally large shell (see Pl. III, fig. 4a, b) and Delessert's illustrations are even larger. The shading is excessively dark and the anterior portion of the aperture is drawn inaccurately. In distinguishing between the two species *costulatus* and *onslowi*, Delessert's figures are at best ambiguous.

4. Bulimus onslowi Cox, 1864

Ann. Mag. nat. Hist. (3) 14: 185. Locality given as Dirk Hartogs Island, Shark Bay, Western Australia (Onslow); Catalogue of specimens of the Australian land shells in the collections of James C. Cox, Sydney, p. 24. Figured in Cox, 1868. A monograph of Australian land shells, Sydney, p. 74, pl. 13, fig.13.

We follow Richardson (1971) in giving priority of publication of the name onslowi Cox to The Annals and Magazine of Natural History. We have examined Cox's type, which bears the Australian Museum registered number C 84882. It corresponds well with the written description, though the dimensions differ slightly from those given by Cox. The illustration is an unlikely reddish-brown whereas the type is yellow-brown and also a little less globose than the figure; the positions of the axial flames more or less correspond. The original label is missing but one, now fragmentary, added by Hedley bears the word 'type' (Mr P.H. Colman, personal communication, 18 January 1972). A further label in Iredale's hand is inscribed 'Not the figured specimen', evidently referring to the fact that another specimen (Western Australian Museum registered number 31-40) was used to illustrate the species in his revision of the genus (Iredale, 1930, pl. II, fig. 19).

The type of *B. onslowi* clearly is a member of the larger of the two Shark Bay species (Pl. V, fig. 1a, b) and is specifically distinct from the type of *Bulimus inflatus* (= costulatus) Lamarck. Cox seems to have been the first to describe this species which, though common on Dirk Hartogs Island and elsewhere on the adjacent mainland, is not known to occur on Bernier (and Dorre) Island, the probable type locality of Lamarck's species.

5. Bothriembryon onslowi var. minor Pilsbry, 1900

Manual of conchology, (2) 13: 12, pl. 3, figs. 45, 46, 47. No locality stated.

After referring to specimens of 'Bulimus (Liparus)' onslowi Cox, collected in 1890-91 by J.J. Walker at Dirk Hartogs Island, Smith (1895: 95) remarked that 'Five other examples are considerably smaller, averaging only 15 to 18 mm in length. They are a trifle less globose and more strongly granular just below the suture'. Smith's shells have been examined by us and are illustrated in Pl. IV, figs. 1-5 and Pl. V, fig. 2a, b. The two largest are B. onslowi; the other five, glued to cardboard, are B. costulatus. Pilsbry (1900: 12) quoted Smith's observation and referred to similar specimens in his own collection, for which he introduced the varietal name minor. Pilsbry described and figured his own two specimens and reproduced the earlier figure of Smith but omitted to state a locality for his own shells.

According to the catalogue of the Academy of Natural Sciences of Philadelphia, Pilsbry's specimens of *B. onslowi* var. *minor* were purchased from Messrs Sowerby and Fulton (Mrs M.C. Rulon, personal communication 17 January 1972) and may have been collected also by J.J. Walker, though there is no positive evidence of this. We have not directly examined Pilsbry's types but, from photographs kindly provided by Mrs Rulon (Pl. III, fig. 6a, b), we believe that they are conspecific with the type material of *costulata* Férussac and *inflatus* (= *costulatus*) Lamarck and specifically distinct from onslowi Cox.

It appears that Pilsbry did not recognize that his shells of 'onslowi var. minor' were conspecific with inflatus (= costulatus) Lamarck because of his confusion of that species with melo Quoy and Gaimard. Then Iredale (1939), having decided mistakenly to apply the name costulatus Lamarck to the larger of the two Shark Bay species of Bothriembryon, raised Pilsbry's varietal name (minor) to full specific rank.

6. Helix (Cochlogena) melones Férussac, 1821

Tableaux Systématiques des animaux mollusques. Limaçons, p. 58, January 1821; p. 54, June 1821. Locality given as: 'La Nouvelle-Hollande'.

This name is a *nomen nudum* and was cited as such in the description of *Helix melo* by Quoy and Gaimard (1832). We do not know of the existence of any specimens which could be confidently regarded as Férussac's original

material but the possibility cannot be excluded that these may have been mixed with Quoy and Gaimard's type series of *H. melo*.

7. Helix melo Quoy and Gaimard, 1832

Voyage de découvertes de l'Astrolabe. Paris. Zoologie 2: 109-111, pl. 9, figs. 4-7 (plates in supplementary atlas). Locality given as: 'au port du Roi-Georges, principalement sur le sommet de Bald-Head' [Summit of Bald-Head, King George Sound].

Quoy and Gaimard evidently derived their name, *melo*, from Férussac's earlier, unavailable name, *melones*, and it seems probable that his specimens were known to them. We have examined a sample of shells from the collection of the Muséum National d'Histoire Naturelle, Paris, which is labelled 'Helix *melones* Fér. Nouvelle Hollande. MM Quoy et Gaimard. 1829'. This sample comprises 11 shells, of which 10 are unquestionably from the Albany district, that is, King George Sound, the other being a Shark Bay shell conspecific with the types of *costulata* Férussac and *inflatus* (= *costulatus*) Lamarck. Within the aperture of the Shark Bay specimen is an adherent deposit of pinkish-brown, calcareous soil, identical with that in shells of the same species from Bernier Island in the collection of the Western Australian Museum. Soils of this nature do not accompany snail shells from the Albany district and, in our experience, do not occur there.

One of the 10 Albany shells bears the inscriptions in black ink 'inflatus 19' and 'melones' but when and by whom these were written is unknown. This shell is the closest of the 10 to Quoy and Gaimard's figures 4 and 5, particularly in the disposition of the axial stripes. However, the height of the figure is proportionately greater than that of the shell and the shading is much darker. (Notwithstanding these differences, we shall nominate this specimen below as the lectotype of Helix melo Quoy and Gaimard.)

Another specimen from the same sample is evidently the white-banded, brown shell (their 'varietas castanea; vitta alba cincta'), illustrated by Quoy and Gaimard's figs. 6 and 7 and to which Pilsbry (1900: 5, fig. 11) referred when introducing his varietal name castaneus. As with the lectotype, the figures of this shell are shaded rather heavily but the proportions of shell and figures agree fairly well.

The type sample of *Helix melo* (excluding the single specimen of *B. costulatus*) compares closely with recently collected samples of that species in the collection of the Western Australian Museum from Bald Head and the adjacent Limestone Head, near Albany. However, the possibility cannot be ruled out that the 10 Paris shells may be a mixture of Quoy and Gaimard's specimens and those of Férussac, which were collected by Péron and Lesueur at King George Sound in 1803. The presence in the sample of one Shark Bay shell, which may well have been collected by Péron and Lesueur but almost

certainly not by Quoy and Gaimard, seems to strengthen the possibility that these represent a combination of Férussac's and Quoy and Gaimard's shells. If so, this would account for the apparent absence in Paris of Férussac's types of *melones*.

Other aspects of the immense confusion that has surrounded the identity of H. melo over the years following its model introduction have been discussed by Iredale (1939). The species is strongly polymorphic in shell characters and this has given rise to a number of varietal names, one of which was elevated to full specific rank by Iredale (1939) as Bothriembryon castaneus Pilsbry, 1900.

8. Bothriembryon inflatus var. castaneus Pilsbry, 1900

Manual of conchology, (2) 13: 5, pl. 1, figs. 11, 18. Bothriembryon castaneus
Pilsbry, 1900. Iredale, 1939. Rec. West. Aust. Mus. 2: 19, pl. 2, fig. 2.
Also published in J. Proc. R. Soc. West. Aust. 25: 19, pl. 2, fig. 2.

Pilsbry (1900) took his description of Bothriembryon 'inflatus var. castaneus' from a shell lent to him by Cox, the locality of which was said to be 'Recherche Archipelago'. Pilsbry's only other record for the variety was Quoy and Gaimard's banded, brown shell from King George Sound, previously discussed, and it is clear that he regarded it merely as one of several forms of a polymorphic species. The Cox-Pilsbry shell, now Australian Museum registered number C 87458, was selected as the type of *B. castaneus* Pilsbry by Iredale (1939: 19), adding that it was 'one of a series from Doubtful Island'. Iredale did not explain how he came by this locality and omitted to mention Pilsbry's earlier citation of the locality 'Recherche Archipelago'. We have examined this specimen and note that of the accompanying labels, only one, in Cox's hand, bears locality data and is inscribed (black-lead pencil) 'Reserch [sic] Archipelago W. Australia'. The shell bears the number 16 in black on the last whorl. There is nothing on the labels to indicate the source of Cox's shell. According to Richardson (1971), he did little personal collecting and relied mainly on exchange and purchase to establish his collection.

The collection of *Bothriembryon* shells from the Recherche Archipelago and coastal localities on the adjacent mainland in the Western Australian Museum comprises 30 lots totalling over 300 shells. We have compared this material with the type of *B. castaneus* and have found that there is no close resemblance between any of them and it. None of the Recherche-Esperance shells features a pale spiral band and we consider that none of them is conspecific with *melo*. On the available evidence we conclude that the Cox-Pilsbry locality, 'Recherche Archipelago', for the type of *castaneus* is probably incorrect. The Australian Museum collection however, contains two lots of shells of *B. melo*, both labelled 'Doubtful Is., King George Sound, W. Aust. R. Helms Coll.'. Lot C 89370 comprises ten pale shells, all axially striped and with a dark, subsutural band and umbilical patch. Lot C 89373 comprises eight brown shells, each with a pale, spiral band. These lots we consider to probably represent the division, according to colour, of what was originally a single sample. We have no other comparative material from Doubtful Island but the shells in Helms' two lots are quite similar to specimens collected recently by one of us (G.W.K.) from the adjacent coast around Bremer Bay.

The type of *B. castaneus* is so similar as to be virtually indistinguishable from Helms' eight shells in lot C 89373 and could very well have been taken from there. According to Hedley (1915), Helms visited Western Australia twice, initially with the Elder Exploring Expedition in 1891-2 and subsequently in 1896-1900. The route of the Elder Expedition did not approach Doubtful Island and it seems more likely that Helms collected his specimens from there some time between 1896 and 1900. In all probability Cox obtained his single, banded shell from Helms during this period, in time for it to be passed on to Pilsbry. Conceivably, the locality discrepancy was acquired by the specimen in passage from Helms to Cox. It seems therefore that Iredale was correct concerning the type locality of *B. castaneus*.

Apart from the foregoing, the type of B. castaneus is typical of some of the more strongly coloured, brown, banded shells of B. melo that occur among populations of that species in the Bremer Bay district and we regard the name as a subjective junior synonym of melo Quoy and Gaimard.

REDESCRIPTIONS

Family Bulimulidae

Genus Bothriembryon Pilsbry, 1894

Liparus Martens (in Albers), 1860. Die Heliceen, second edition, p. 229 non Liparus Olivier, 1807 (Insecta), nec Liparus Albers 1850.

Bothriembryon Pilsbry, 1894. The Nautilus 8: 35-36.

Bothriembryon Pilsbry, 1900. Manual of conchology, (2). Pulmonata. 13:1.

Type species

By original designation, Bulimus melo (Quoy and Gaimard) = Helix melo Quoy and Gaimard.

Generic diagnosis

Bulimulid snails of small to large size, elevated, elongate-ovate to globoseconical, whorls convex, sutures impressed, finely crenulated; sculpture of uneven, wrinkled, transverse growth striae, flexed and accentuated below the suture and usually bearing or crossed by spiral chords of variable strength, more prominent on the posterior third. Aperture oval, oblique, discontinuous, the margins joined by a thin parietal glaze; inductura finely granose; outer lip thin, slightly prosocline and sinuate; columella reflected, without folds; umbilicus small or closed. Protoconch of 1.5 to 2.5 whorls, terminally descending, with fine axial and/or reticulate sculpture, distinct from that of the teleoconch. The form of the protoconch distinguishes the genus from all other known land snails from the Australasian Region. Colours of the teleoconch comprise shades of yellow, brown, red, lilac and white, often in patterns of irregular axial flames and less frequently, spiral bands.

Anatomy

The jaw is arcuate and plaited, the median segment triangular or wedgeshaped; radula about as in *Bulimulus*; genital system simple, much as in *Bulimulus* (Pilsbry, 1900).

The anatomy of a specimen, referred to *B. inflatus* (Lamarck) on a determination by C. Hedley, was described in some detail by Pilsbry (1946). This may have been a specimen of *B. melo* but no locality is indicated and the identity of the specimen is uncertain. An earlier anatomical study of *'Bulimulus' melo* (Quoy and Gaimard) is by Semper (1870: 154, taf. XV, fig. 14, taf. XVII, fig. 13).

Geographic range

Western Australia, from the entire southern coast, northward to the Hamersley Range; southern South Australia from Eyre Peninsula westward and Kangaroo Island; Northern Territory at Palm Valley near Hermannsburg; Tasmania.

Stratigraphic range

? Miocene to Recent (Ludbrook, 1963; McMichael, 1968).

Remarks

In proposing the new name Bothriembryon, Pilsbry (1894) cited as type species Bulimus melo (Quoy and Gaimard) but in later studies (Pilsbry 1900, 1946) used the name inflatus Lamarck when referring to that species. In this, he seems to have been influenced by the views of Hedley (1892, 1895, 1916). Of the subgenera of Iredale (1933, 1939), the earlier group, Tasmanembryon, Hartogembryon, Larapintembryon and Satagembryon were based on observations by Pilsbry (1900) on interspecific differences in protoconch sculpture. The later group, Dialembryon, Ponembryon, Telembryon and Celatembryon, appear to be based on little more than size in the case of the first two, the others being undefined beyond citation of the respective type species, B. kingii (Gray) and B. distinctus Iredale.

Iredale (1939) himself expressed uncertainty and also some inconsistency in attempting to arrange the species of *Bothriembryon* into subgenera and it is apparent that the question requires further study. This being beyond the scope of the present work, we shall confine ourselves to the observation that protoconch sculpture may need to be assessed in conjunction with other characters in determining subgeneric relationships.

Shell dimensions

In the present study, shell whorls have been counted under magnification by orientating the specimen so that the terminal lobe of the protoconch is directed toward the viewer, as in fig. 1. Whorls increase with each subsequent intersection by the suture of a line descending from the terminal lobe; tenths of whorls have been estimated. Shell height has been determined as the distance from the apical to the basal extremity. Maximum width represents the distance from the outer lip to the farthest edge of the last whorl, measured normal to the shell axis.



Fig. 1: Shell orientation for counting whorls, beginning with the protoconch. Arrow indicates direction of growth.

Bothriembryon melo (Quoy and Gaimard) (Pl. I, II, III figs 1a, b, 2a, b, 3a, b. Map 2)

- Helix melo Quoy and Gaimard, 1832. Voyage de découvertes de l'Astrolabe. Paris. Zoologie 2:109. Supplementary atlas, pl. 9, figs. 4-7.
- Liparus inflatus var. melo (Quoy and Gaimard). Hedley, 1892. Rec. Aust. Mus. 2: 29.

Bothriembryon melo (Quoy and Gaimard). Pilsbry, 1894. Nautilus 8: 36.

Bothriembryon inflatus (Lamarck). Pilsbry, 1900. Manual of conchology. (2). Pulmonata. 13: 3-6, pl. 1, figs. 1-5 (part).

Bothriembryon inflatus (Lamarck). Hedley, 1916. J. Proc. Roy. Soc. West. Aust. 1: 216 (part).

Bothriembryon castaneus Pilsbry. Iredale, 1939. Rec. West. Aust. Mus. 2: 19, pl. 2, fig. 2; also published in J. Proc. Roy. Soc. West. Aust. 25: 19, pl. 2, fig. 2.

Type locality

Summit of Bald Head, King George Sound. Located on the extremity of the Flinders Peninsula, south of Albany across King George Sound, this site now lies within the Torndirrup National Park.

Type series

Museum National d'Histoire Naturelle, Paris. Lectotype and 9 paralectotypes, here selected; unregistered.

| Dimensions (mm) | (a) | (b) | (c) | (d) | (e) |
|--------------------|------|------|------|------|------|
| Height of shell | 25.2 | 22.3 | 22.3 | 30.7 | 27.0 |
| Height of aperture | 13.9 | 12.6 | 12.4 | 15.7 | 15.0 |
| Maximum width | 15.0 | 12.8 | 12.9 | 17.3 | 15.2 |
| No. of whorls | 5.4 | 5.2 | 5.2 | 5.8 | 5.4 |
| Protoconch whorls | 1.9 | 1.9 | 1.8 | 1.8 | 2.0 |

- (a) Lectotype, from Bald Head near Albany.
- (b) Paralectotype, also from Bald Head. Quoy and Gaimard's shell 'varietas castanea, vitta alba cincta'.
- (c) Holotype of *B. castaneus* Pilsbry, probably from Doubtful Island. Australian Museum C 87458.
- (d) A large shell from Bald Head near Albany. Western Australian Museum 247-72 (part).
- (e) A large shell from near the seaward part of the Hunter River estuary. Western Australian Museum 266-70 (part).

Diagnosis

A Bothriembryon of medium size, ovate-conical, with 5 whorls in a height of 21-23 mm and a height to width ratio of about 5 to 3. Sculpture of weak transverse growth striae, accentuated below and crenulating the suture; crossed by spiral chords, usually weak and confined to the posterior third, becoming obsolete on the last whorl; periostracum thin. Protoconch of 1.7 to 2.1 whorls, initially sculptured with fine, anastomose axial wrinkles passing into an irregular reticulate sculpture with a tendency to axial alignment; the last 0.1-0.2 whorl usually with fine, close anastomose, axial wrinkles; base of the protoconch very finely granose or almost smooth, polished; colour a light to medium brown, without axial flames. Teleoconch of one or more colours, shades of brown, yellow and white in combinations of diffuse, axial and/or spiral patterns; a white-flecked, chestnut, subsutural band and a chestnut umbilical patch are commonly present; with or without axial flames.

Morphs

Some distinctive common colour morphs known to us are here listed. Intermediate-coloured shells also occur.

(a) Off-white to yellowish-brown with a prominent, white-flecked, chestnut, subsutural band and brown axial stripes which converge into a brown, umbilical patch; columella pinkish-brown, lilac or white; usually without axial flames, but occasionally with obscure pale yellow flames. The lectotype is a weathered example of this form, which is common at Bald Head, Limestone Head, Frenchman Bay, Breaksea Island, Cheyne Beach and other localities near Albany; occasionally appears at Bremer Bay (Pl. I, figs. 1a, b, 4a, b, 6a, b, Pl. II, fig. 2a, b).

(b) Pale yellow, with a chestnut-brown, subsutural band, strong to weak; without axial flames; umbilicus brown; columella shades of brown, pink or lilac. Occurs at Frenchman Bay near Albany (Pl. 11, fig. 1a, b).

(c) Diffuse olive brown, with or without a chestnut subsutural band and umbilical patch; without axial flames; columella pale brown. Occurs in the valley of the Waychinicup River, east of Albany (Pl. 11, fig. 6a, b).

(d) Straw-yellow, with or without weak brown axial streaks, subsutural band and umbilical patch; with or without obscure, pale, axial flames; columella whitish to brown. Occurs on Bald and Breaksea Islands, Two Peoples Bay and the vicinity of the Angove River pumping station (Pl. 11, fig. 5a, b).

(e) Diffuse chestnut to dark brown, usually with, but occasionally without, one or two peripheral bands, which may be visible on the spire; generally without axial flames but these are occasionally present [see (h)]. Present in both relatively slender and wide shells. Occurs at Bald Head, Limestone Head, Frenchman Bay, Nanarup, Two Peoples Bay and the Bremer Bay district. Corresponds to Quoy and Gaimard's white-banded brown shell from Bald Head. Similar shells from the Bremer Bay district more often feature yellow axial flames, being exemplified by the type of *B. castaneus* Pilsbry Pl. I, figs. 2a, b, 3a, b. Pl. II, fig. 4a, b, Pl. III, fig. 3a, b).

(f) Similar to (a), but with 1 to 3 white peripheral bands. Occurs at Bald Head, Limestone Head, Frenchman Bay and other localities near Albany (Pl. 1, fig. 5a, b, Pl. 11, 3a, b).

(g) Similar to (a), but darker, with more intense colours and yellowish axial flames. Occurs in the Bremer Bay district near Wellstead Estuary (Pl. III, fig. 1a, b).

(h) Similar to (e), intense dark to tan brown with well-developed, thin yellow axial flames, with or without a pale, peripheral spiral band. Occurs on Bald Island and near the Hunter River estuary (Pl. III, fig. 2a, b).

Geographic range

Numerous localities, all near the coast from Tor Bay, west of Albany to Point Charles near Fitzgerald Inlet; also Michaelmas, Breaksea, Bald and Doubtful Islands (Map 2). Commonly on dunes with a cover of heath vegetation or *Agonis* thickets; occasionally found on heavier soils overlying gneissic rocks. Frequently sympatric with *B. kingii* (Gray).

The fossil collection of the Western Australian Museum contains specimens of *B. melo* collected in association with remains of the extinct marsupial *Zygomaturus trilobus* from lithified soils developed on Late Quaternary aeolian calcarenites near Bremer Bay (Merrilees, 1970). *B. melo* has also been collected from a similar fossil soil horizon at Limestone Head.

> Bothriembryon costulatus (Lamarck) (Pl. III, figs. 4a, b, 5a, b, 6a, b, Pl. IV. Map 3)

- Bulimus inflatus Lamarck, 1822. Histoire naturelle des animaux sans vertèbres 6: 122. Non Bulimus inflatus Olivier, 1801.
- Helix costulata Lamarck, 1822. Histoire naturelle des animaux sans vertebres 6: 122. From synonymy.
- Helix (Cochlogena) costulata Férussac, 1821. Tableaux systematiques des animaux mollusques. Limaçons, pp. 54, 58. Nomen nudum.
- Bulimus inflatus Lamarck. Delessert, 1841. Recueil de coquilles décrites par Lamarck, pl. 28, fig. 1.
- Bulimus (Liparus) onslowi Cox. Smith, 1895. Proc. malac. Soc. Lond. 1: 95 (part).
- Bothriembryon onslowi var. minor Pilsbry, 1900. Manual of conchology (2). Pulmonata. 13: 12, pl. 3, figs. 45, 46, 47.
- Bothriembryon minor Pilsbry. Iredale, 1939. Rec. West. Aust. Mus. 2: 27, pl. 2, fig. 20; also published in J. Proc. Roy. Soc. West. Aust. 25: 27, pl. 2, fig. 20.
- Bulimus inflatus Lamarck. Mermod, 1951. Revue suisse Zool. 58: 728-729, fig. 78.

Type locality

New Holland = probably Bernier Island, Shark Bay, Western Australia. Type series

Muséum d'Histoire Naturelle, Geneva. Lamarck Collection, lectotype and 4 paralectotypes; the former, number 1092/65.

The lectotype has been described and figured by Mermod (1951: 728-729, fig. 78). With 5.8 whorls in a height of 26.0 mm, it is exceptionally large for the species. The whole shell is worn and faded a dull off-white but

appears to have had originally a light brown ground colour with spaced, white axial flames; the protoconch shows no trace of axial flames. A quantity of loose, pink-brown sand has become dislodged from within the shell and has been retained with it.

Dimensions (mm)

Note: These are NOT the dimensions of the 'Type series'.

| | (a) | (b) | (c) | (d) | (e) |
|--------------------|------|------|------|------|------|
| Height of shell | 26.0 | 21.9 | 14.5 | 22.1 | 19.9 |
| Height of aperture | 14.2 | 11.7 | 8.0 | 11.9 | 10.4 |
| Maximum width | 15.7 | 12.1 | 8.2 | 14.2 | 10.4 |
| No. of whorls | 5.8 | 5.5 | 5+ | 5.5 | 5.3 |
| Protoconch whorls | 2.2 | 1.9 | | 2.2 | 2.1 |

(a) Lectotype, probably from Bernier Island.

- (b) The largest of Férussac's 7 shells, probably also from Bernier Island.
- (c) The larger of the type series of *minor* Pilsbry (dimensions from text). Precise locality unknown.
- (d) A large shell from 16 miles south of Point Cloates (northern population).
- (e) From Red Bluff, 5 miles south of the mouth of the Murchison River (southern population).

Diagnosis

A Bothriembryon of medium size, ovate-conical to globose-conical, with 5 whorls in a height of 14-20 mm (see fig. 2) and a height to width ratio of about 3 to 2. Sculpture of weak, transverse growth striae bearing fine, granose, spiral chords on the posterior third; periostracum thin. Protoconch of 1.9 to 2.3 whorls bearing fine, close, wavy, axial wrinkles, occasionally becoming reticulate on the second whorl; colour brown, often darker than the teleoconch and with white, axial flames appearing at about 1.5 whorls. Teleoconch colours generally rather pallid, beige or medium brown, occasionally with pink or yellow tones, broken by white, irregular axial flames; sometimes a dull off-white or a diffuse pale-brown, without axial flames; columella white; often with a white circumbilical band, weakly or strongly defined; aperture coloured within like the exterior, but more intensely, the lip broadly edged in white. Axial flames persist in bleached, faded shells, such as the type.

Geographic range

Numerous localities, all near the coast, from 16 miles south of Point Cloates to Red Bluff, 5 miles south of Kalbarri; also Bernier, Dorre, Dirk Hartogs, Baudin and Salutation Islands in Shark Bay (Map 3). Associated with heath, Triodia and Acacia vegetation on well-drained, pale to reddishbrown sandy soils and occasionally on limestone outcrops. Sympatric with B. onslowi throughout Edel Land, Péron Peninsula and Dirk Hartogs Island.



Fig. 2: Graph showing the relationship of shell height to number of whorls in *B. onslowi* and *B. costulatus*. Specimens of onslowi from Dirk Hartogs Island; Monkey Mia, Peron Peninsula; Carrarang-Tamala boundary near the western coast; 2 miles north of Billabong roadhouse, North West Coastal Highway, False Entrance Well, Carrarang. Specimens of costulatus from Bernier Island; Dirk Hartogs Island; 2 miles south of Pt Maud, Cardabia; False Entrance Well, Carrarang; vicinity of Zuytdorp wreck 40 miles (65 km) north of Kalbarri.

The fossil collection of the Western Australian Museum contains samples of B. costulatus from Bernier and Dorre Islands, Edel Land, Peron Peninsula, the vicinity of Tamala, Point Quobba and the site of the 'Zuytdorp' wreck some 65 km (40 miles) north of Kalbarri. These have been collected from both unlithified, modern soil profiles and from well lithified Pleistocene fossil soils (see Logan et al., 1970: 68). Shells of B. costulatus from these older deposits tend to be larger than modern shells, some even exceeding the type, which is the largest known modern specimen. In some localities, these large fossil specimens are associated with shells of what appear to be two extinct species of Bothriembryon, including that noted by Ride (1962: 24-25) on Dorre Island and probably by Péron (1807: 110-111) on Bernier Island. B. onslowi is not known to occur in the same deposits as these fossil species.

The volume of fossil evidence at present available is not enough for firm conclusions to be drawn but suggests that *B. costulatus* may have inhabited the district for longer than *B. onslowi*. The greater size of some of the Pleistocene shells of *costulatus* compared with modern specimens may point to adverse environmental changes since then. The apparent extinction of two species of *Bothriembryon* in the district since the Pleistocene seems to be consistent with such changes.

The affinities of costulatus appear to lie with a group of species, characterized by the presence of pale axial flames on the protoconch, located mainly in the south coast and lower south-west regions of the State. The group includes *B. brazieri* (Angas), *B. kingii* (Gray) and others; an undescribed species from Pt D'Entrecasteaux has similar protoconch sculpture to that of costulatus.

Bothriembryon onslowi (Cox) (Pl. V. Map 4)

Bulimus onslowi Cox, 1864. Ann. Mag. nat. Hist. (3) 14: 185.

Bulimus onslowi Cox, 1864. Catalogue of specimens of the Australian land shells in the collections of James C. Cox, Sydney. J.A. Engel, p. 24.

Bulimus onslow Cox. Cox, 1868. A monograph of Australian land shells. Wm Maddock, Sydney. p. 74, pl. 13, fig. 13.

Bothriembryon costulatus (Lamarck, 1822). Iredale, 1939. Rec. West. Aust.
 Mus. 2: 26-27, pl. 2, fig. 19; also published in J. Proc. Roy. Soc. West.
 Aust. 25: 26-27, pl. 2 fig. 19.

Type locality

Dirk Hartogs Island, Western Australia.

Туре

Australian Museum, Sydney, number C 84882.

| Dimensions (mm) | (a) | (b) | (c) | (d) | (e) |
|--------------------|------|------|------|------|------|
| Height of shell | 21.1 | 30.4 | 21.0 | 18.3 | 25.2 |
| Height of aperture | 13.3 | 18.2 | 13.2 | 10.8 | 15.9 |
| Maximum width | 14.1 | 18.5 | 13.8 | 12.1 | 16.1 |
| No. of whorls | 4.7 | 5.4 | 5.0 | 4.8 | 5.2 |
| Protoconch whorls | 1.7 | 2.0 | 1.9 | 1.8 | 1.9 |

(a) Holotype.

(b) A large shell from near the coast at the Carrarang-Tamala boundary. Western Australian Museum 225-73 (part).

- (c) From Monkey Mia, Peron Peninsula. Western Australian Museum 226-73 (part).
- (d) From beside North West Coastal Highway 47 km south of the Shark Bay turn-off. Western Australian Museum 224-73 (part).
- (e) From Dirk Hartogs Island. Iredale's figured specimen. Western Australian Museum 31-40 (part).

Diagnosis

A Bothriembryon of medium size, ovate-conical, with 5.0 whorls in a height of 20-27 mm (see fig. 2) and a height to width ratio of about 3 to 2. Sculpture of weak, transverse, growth striae bearing fine granose spiral chords above the periphery; periostracum thin. Protoconch of 1.7 to 2.2 whorls, sculptured initially with obscure, irregular, axial wrinkles; after the first half whorl, becoming more or less reticulate, often with a marked axial alignment; the last 0.1-0.3 whorl with fine, close, axial wrinkles; colour light brown, paler than the teleoconch and without axial flames. Teleoconch colours generally rather intense, chestnut-brown, interrupted by irregular, off-white to yellow-brown axial flames; columella white. Aperture coloured within like the exterior but more diffuse, the lip narrowly edged in white. Axial flames persist in bleached, faded shells. In life, the axial flames may be greenish-yellow.

Geographic range

Dirk Hartogs Island, Edel Land, Péron Peninsula and adjacent areas near Shark Bay. Associated with well-drained sandy soils with heath and *Acacia* vegetation. Sympatric with *B. costulatus* throughout most of the known range.

The fossil collection of the Western Australian Museum contains samples of *B. onslowi* from what appear to be modern (i.e., post-Pleistocene) soil profiles in Edel Land, Péron Peninsula and the vicinity of Tamala. There is, in addition, a single shell, apparently of this species, from Useless Loop, embedded in the calcrete of a weathered soil profile. These records all lie within the known modern range of the species and all associated species are extant. The stratigraphic range is possibly late Pleistocene to Recent.

The affinities of *onslowi* appear to lie with species such as *melo* and *bulla* (of the Perth district) in which the protoconch lacks axial flames. In protoconch sculpture, *onslowi* and *melo* are somewhat similar and their ratios of height to number of whorls are sometimes comparable.

| This pape | cost ula tus | melo | onstown |
|------------------------------|---|----------------------|-------------------|
| Iredale, 1939 | minor | melo | costulatus |
| Hedley, 1916 | | inflatus (part) | onsiowi |
| Pilsbry, 1900 | onsłowi var. minor | inflatus (part) | imotsuo |
| Smith, 1895 | onsłowi (part) | melo (part) | onslowi (part) |
| Pilsbry, 1894 | | melo | |
| Hedley, 1892 | | inflatus var melo | imotsuo |
| Cox, 1868 | ınf la tus | melo | onstowi |
| Cox, 1864 | inflatus | meto | onstowi |
| Albers, 1860 | in flat us | melo | |
| Quoy and Gaimard, 1832 | | melo | |
| Lamarck, 1822 | inflatus preoccupied) = costulata in synonymy) | | |

Table 1. A comparison of usages of the names inflatus Lamarck (= costulata Lamarck), melo Quoy and Gaimard and onslowi Cox from various sources.

| | melo | costulatus | onslowi |
|---|---|--|---|
| Maximum height. | About 30 mm. | Rarely greater than 23 mm (fossils may reach 27 mm). | About 30 mm; often greater than 23 mm. |
| Height to width ratio. | About 5: 3. | About 3:2; tends to be a little more elevated than <i>onslowi</i> . | About 3:2. |
| Whorls to height. | 5 whorls in 21-23 mm. | 5 whorls in 14-20 mm. | 5 whorls in 20-27 mm. |
| Teleoconch colours, fresh shells. | Variable patterns and shades of brown, yellow and white, spiral and/or axial; chestnut subsutural band and umbilical patch common. | Usually pallid; brown to off-white, occasionally with pink or yellow tones; diffuse or with axial flames; white spiral band often present on the base. | Intense brown with yellow-brown axial flames; spiral patterns absent; shells containing the live animal may show a greenish hue. |
| Protoconch colours. | Brown, without axial flames. | Brown, often darker than the teleo- conch, and with white axial flames on the second whorl. | Brown, paler than the teleoconch, and without axial flames. |
| Protoconch whorls. | 1.7-2.1 whorls. | 1.9-2.3 whorls, generally more than in <i>onslowi</i> . | 1.7-2.2 whorls, generally fewer than in costulatus. |
| Protoconch sculpture. | Initially with fine, anastomose axial wrinkles, passing into an irregular, reticulate sculpture with a tendency to axial alignment; the last 0.1-0.2 whorl usually with fine, close, anastomose axial wrinkles. | Fine, close, wavy, axial wrinkles throughout, occasionally becoming reticulate on the second whorl. | Initially with obscure, irregular, axial wrinkles; after the first half whorl, becoming more or less re- ticulate, often with a marked axial alignment; the last 0.1-0.3 whorl with fine close axial wrinkles. |

Table 2. Comparison of diagnostic shell characters of Bothriembryon melo,B. costulatus and B. onslowi.

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